The Collapse of the California Sardine Fishery

What Have We Learned?

JOHN RADOVICH

Abstract

For a number of years, Federal scientists, employed by an agency whose primary goal was to assist the development of the U.S. commercial fisheries, looked for causes, other than fishing, for the Pacific sardine's decline, while California State scientists, charged with the role of protector of the State's resources, sought reasons to support the premise that overfishing was having an effect. At the same time, scientists from Scripps Institution of Oceanography looked for fundamental generalizations in theory rather than the activities of man to explain changes in fish populations. For many years, California State personnel struggled without success to gain control over a burgeoning, and later declining sardine fishery.

Faced with the possibility that legislation might be enacted, giving the California Fish and Game Commission control over the sardine fishery, the California fishing industry sponsored the formation of the Marine Research Committee to collect and disburse funds and to coordinate and sponsor more "needed" research, thereby forestalling any action to allow management of the fishery to come under the authority of the California Fish and Game Commission. Subsequently, the California Cooperative Oceanic Fisheries Investigations (CalCOFI) was formed, under which cooperative research proceeded.

Oceanic conditions (temperature) was found to affect profoundly the distribution, year-class production, and yield of sardines. Nonintermingling or only partially intermingling stocks of sardines have been described. Considerable attention has been focused on the complementary role of sardines and anchovies as competing species acting as a single biomass while competing with each other as part of that biomass. Confirmation of this hypothesis was found to have been based on faulty interpretation of basic data. If such a relationship exists, it still needs to be demonstrated. Density-controlling mechanisms, however, which may be of greater importance, include predation, cannibalism, and other behavioral characteristics. Schooling behavior, for instance, which has evolved through natural selection to decrease mortality from predation, may work toward destruction of the prey species when it is confronted by a fishery which evolves more rapidly than does the species defense against it. A model that is consistent with the results of all the previous studies on the sardine must bring one to the conclusion that the present scarcity of sardines off the coast of California, and their absence off the northwest, is an inescapable climax, given the characteristics and magnitude of the fishery and the behavior and life history of the species.

INTRODUCTION

At a symposium of the CalCOFI conference held in La Jolla, California, on December 5, 1975, on "The Anchovy Management Challenge," a paper was presented by W. G. Clark on "The Lessons of the Peruvian Anchoveta Fishery."[1] It is ironic that California's anchovy researchers felt compelled to learn lessons from the collapse of the Peruvian fishery

---

Reprinted by permission. From the book *Resource Management and Environmental Uncertainty: Lessons from Coastal Upwelling Fisheries*, edited by Michael H. Glantz and J. Dana Thompson. A Wiley-Interscience Publication, John Wiley & Sons, New York, 1981.

which the Pacific sardine's failure could have provided to them as well as to the Peruvian anchoveta researchers. The observations which follow are presented with the hope that a discussion of some of the social, political, and biological factors associated with the decline of the California sardine fishery will have useful applications in interpreting events now taking place in our fisheries.

After 50 years of fishing for the Pacific sardine, *Sardinops sagax* (Jenyns), a moratorium on landings was imposed by the California Legislature in 1967, thus bringing to an end yet another act of one of the more emotionally charged fisheries exploitation-conservation controversies of the 20th century.

By the time the moratorium was imposed, however, the sardine fishery in southern California had already collapsed. The sardine fisheries in the northwest had long since ceased to exist with sardines last landed in British Columbia in the 1947–1948 season, in Oregon and Washington in the 1948–1949 season, and in San Francisco Bay in the 1951–1952 season (Table 1).

Even before the productivity and exploitation of the fishery peaked, researchers from the (then) California Division of Fish and Game issued warnings that the commercial exploitation of the fishery could not increase without limits, and recommended that an annual sardine quota be established to keep the population from being overfished.

Such recommendations were, of course, opposed by the fishing industry which was able to identify scientists who would state, officially or otherwise, that it was virtually impossible to overfish a pelagic species. This debate permeated the philosophies, research activities, and conclusions of the scientists working in this field at that time. The debate conformed to the basic charters (or *raisons d'être*) of each agency involved and persists today, long after the United States Pacific sardine fishery has ceased to exist. As a result of deep-rooted social and political feelings concerning the collapse of the Pacific sardine off California, many conflicting hypotheses have arisen, in spite of the completion of a vast amount of research.

For example, just recently, a prominent representative of a major oceanographic research institution asserted that it was a "false assumption that overfishing killed the former sardine fishery off Northern California. . . . The real cause of the disappearance of the California sardine was a climatic change."[2] The same official, addressing a group of scientists, stated that

> . . . the explanation of the disappearance [of the sardine] seems to be a change of climate that triggered a major biological upheaval. It was very quiet by our standards, we who live in the atmosphere, but it was violent in that several million tons of one species was replaced by another [anchovy].[3]

If this view is valid, one must ask why scientists of the California Department of Fish and Game supported a moratorium on fishing for sardines. Why did they recommend quotas of 250,000 to 300,000 tons of sardines as a measure to forestall the collapse which they had predicted would occur?[4] MacCall recently postulated that a safe estimate of the maximum sustainable yield (MSY) for the Pacific sardine, assuming it were to be rehabilitated, would be about 250,000 metric tons and that if the catch had been held to that limit the fishery would still be viable.[5]

TABLE 1. Seasonal Catch (tons) of Sardines along the Pacific Coast (Each Season Includes June through the Following May[a])

	Pacific Northwest				California							
					Northern California							
Season	British Columbia	Washington	Oregon	Total	Reduction Ships	San Francisco	Monterey	Total	Southern California	Total California	Baja[c] California	Grand Total
1916–1917	—	—	—	—	—	—	7,710	7,710	19,820	27,530	—	27,530
1917–1918	80	—	—	80	—	70	23,810	23,880	48,700	72,580	—	72,660
1918–1919	3,640	—	—	3,640	—	450	35,750	36,200	39,340	75,540	—	79,180
1919–1920	3,280	—	—	3,280	—	1,000	43,040	44,040	22,990	67,030	—	70,310
1920–1921	4,400	—	—	4,400	—	230	24,960	25,190	13,260	38,450	—	42,850
1921–1922	990	—	—	990	—	80	16,290	16,370	20,130	36,500	—	37,490
1922–1923	1,020	—	—	1,020	—	110	29,210	29,320	35,790	65,110	—	66,130
1923–1924	970	—	—	970	—	190	45,920	46,110	37,820	83,930	—	84,900
1924–1925	1,370	—	—	1,370	—	560	67,310	67,870	105,150	173,020	—	174,390
1925–1926	15,950	—	—	15,950	—	560	69,010	69,570	67,700	137,270	—	153,220
1926–1927	48,500	—	—	48,500	—	3,520	81,860	85,380	66,830	152,210	—	200,710
1927–1928	68,430	—	—	68,430	—	16,690	98,020	114,710	72,550	187,260	—	255,690
1928–1929	80,510	—	—	80,510	—	13,520	120,290	133,810	120,670	254,480	—	334,990
1929–1930	86,340	—	—	86,340	—	21,960	160,050	182,010	143,160	325,170	—	411,510
1930–1931	75,070	—	—	75,070	10,960	25,970	109,620	146,550	38,570	185,120	—	260,190
1931–1932	73,600	—	—	73,600	31,040	21,607	69,078	121,725	42,920	164,645	—	238,245
1932–1933	44,350	—	—	44,350	58,790	18,634	89,599	167,023	83,667	250,690	—	295,040
1933–1934	4,050	—	—	4,050	67,820	36,336	152,480	256,636	126,793	383,429	—	387,479
1934–1935	43,000	—	—	43,000	112,040	68,477	230,854	411,371	183,683	595,054	—	638,054
1935–1936	45,320	10	26,230	71,560	150,830	76,147	184,470	411,447	149,051	560,498	—	632,058
1936–1937	44,450	6,560	14,200	65,210	235,610	141,099	206,706	583,415	142,709	726,124	—	791,334
1937–1938	48,080	17,100	16,660	81,840	67,580	133,718	104,936	306,234	110,330	416,564	—	498,404
1938–1939	51,770	26,480	17,020	95,270	43,890	201,200	180,994	426,084	149,203	575,287	—	670,557
1939–1940	5,520	17,760	22,330	45,610	—	212,453	227,874	440,327	96,939	537,266	—	582,876
1940–1941	28,770	810	3.160	32,740	—	118,092	165,698	283,790	176,794	460,584	—	493,324
1941–1942	60,050	17,100	15,850	93,000	—	186,589	250,287	436,876	150,497	587,373	—	680,373
1942–1943	65,880	580	1,950	68,410	—	115,884	184,399	300,283	204,378	504,661	—	573,071
1943–1944	88,740	10,440	1,820	101,000	—	126,512	213,616	340,128	138,001	478,129	—	579,129
1944–1945	59,120	20	—	59,140	—	136,598	237,246	373,844	181,061	554,905	—	614,045
1945–1946	34,300	2,310	90	36,700	—	84,103	145,519	229,622	174,061	403,683	—	440,383
1946–1947	3,990	6,140	3,960	14,090	—	2,869	31,391	34,260	199,542	233,802	—	247,892
1947–1948	490	1,360	6,930	8,780	—	94	17,630	17,724	103,617	121,341	—	130,121
1948–1949	—	50	5,320	5,370	—	112	47,862	47,974	135,752	183,726	—	189,096
1949–1950	—	—	—	—	—	17,442	131,769	149,211	189,714	338,925	—	338,925
1950–1951	—	—	—	—	—	12,727	33,699	46,426	306,662	353,088	—	353,088
1951–1952	—	—	—	—	—	82	15,897	15,979	113,125	129,104	16,184	145,288
1952–1953	—	—	—	—	—	—	49	49	5,662	5,711	9,162	14,873
1953–1954	—	—	—	—	—	—	58	58	4,434	4,492	14,306	18,798
1954–1955	—	—	—	—	—	—	856	856	67,609	68,465	12,440	80,905
1955–1956	—	—	—	—	—	—	518	518	73,943	74,461	4,207	78,668
1956–1957	—	—	—	—	—	—	63	63	33,580	33,643	13,655	47,298
1957–1958	—	—	—	—	—	—	17	17	22,255	22,272	9,924	32,196
1958–1959	—	—	—	—	—	—	24,701	24,701	79,270	103,971	22,334	126,305
1959–1960	—	—	—	—	—	—	16,109	16,109	21,147	37,256	21,446	58,702
1960–1961	—	—	—	—	—	—	2,340	2,340	26,538	28,878	19,899	48,777
1961–1962	—	—	—	—	—	—	2,231	2,231	23,297	25,528	21,270	46,798
1962–1963	—	—	—	—	—	—	1,211	1,211	2,961	4,172	14,620	18,792
1963–1964	—	—	—	—	—	—	1,015	1,015	1,927	2,942	18,384	21,326
1964–1965	—	—	—	—	—	—	308	308	5,795	6,103	27,120	33,223
1965–1966	—	—	—	—	—	—	151	151	568	719	22,247	22,966
1966–1967	—	—	—	—	—	—	23	23	321	344	19,531	19,875
1967–1968	—	—	—	—	—	—	—	—	71	71	27,657	27,728

[a] British Columbia data were supplied by the Canadian Bureau of Statistics and the province of British Columbia; Washington data by the Washington Department of Fisheries; and Oregon data by the Fish Commission of Oregon. Deliveries to reduction ships and data for Baja California were compiled by the United States Fish and Wildlife Service from records of companies receiving fish. California landings were derived from records of the California Department of Fish and Game.

[b] Prior to the 1931–1932 season, fish landed in Santa Barbara and San Luis Obispo Counties are included in southern California. Subsequent landings north of Point Arguello are included in Monterey and those south of Point Arguello are included in southern California.

[c] The amount of sardines landed in Baja California prior to the 1951–1952 season is not known.

Clearly, these views conflict. Why, and to what extent, do these conflicting views persist in scientific circles? Which concepts are in error? What seems to be the truth? The complete answers to these questions, particularly to the last one, are beyond the scope of this paper. However, it is time to recall a few pertinent events which may improve the historical perspective and provide better insights for the interpretation of the mass of ecological data already accumulated.

HISTORICAL REVIEW

Differences in Agency Perspective

The California Fish and Game Commission began with the approval of an act of the California Legislature creating the Commissioners of Fisheries on April 2, 1870, by Governor Haight of California. The principal purpose of the Commission was embodied in the title of the legislation, "An act to provide for the restoration and preservation of fish in the waters of this State." While the objectives of the California Fish and Game Commission and its Department of Fish and Game have expanded since then, their role as protector of the State's fish and wildlife resources has remained paramount.

In 1871 the U.S. Bureau of Commercial Fisheries was created; the primary goal of the new Federal Bureau was to assist in the development and perpetuation of the United States fishing industries. This goal persists today, despite several agency name changes, even though the present National Marine Fisheries Service (NMFS) too has broadened its objectives somewhat in recent years.

For many years, federal personnel from the National Marine Fisheries Service debated vigorously with personnel from the California Department of Fish and Game on what was happening to the Pacific sardine. The Federal scientists, working for an agency whose fundamental charter was to assist the development and maintenance of U.S. commercial fisheries, looked for reasons other than fishing, for the sardine's declining condition, while the scientists employed by the State (whose basic role was protector of the State's resources) supported the premise that overfishing was having a detrimental effect on the standing stock. These were capable, competent scientists using the same data and coming up with different conclusions in part because they were employed by agencies whose fundamental goals were different.

Scientists are directly and indirectly influenced by the values of their society, their institutions, their academic disciplines, as well as by their personal political beliefs. Each scientific discipline is saturated with values imposed by its specific profession, and scientists are influenced by the agencies for which they work and to which they owe some allegiance. Thus, the definition of a problem becomes a biological one, a physical one, an economic one, a psychological one, a sociological one, even a philosophical one, depending on the researcher's discipline.

As another example, oceanographers frequently define their field as encompassing the ocean and all the sciences that are studied in relation to the ocean. This all-inclusive perspective relegates other sciences (biology, chemistry, physics, and geology) to the position of subdisciplines of oceanography. Such a disciplinary perspective tends to focus attention away from the effects of local human activities on various marine resources and to extend efforts, instead, toward the investigation of large-scale processes in search of fundamental generalizations to explain widespread phenomena. One might argue that an elitism tends to develop, where one finds, for the example given, at the top of the scale the physical oceanographer, and at the bottom, the biological oceanographer. Carrying this example one step further, perhaps because marine plankton is more dependent on currents, temperature, and other physical and chemical processes, phytoplanktonologists tend to be more influential than other biological oceanographers. Oceanographic institutions usually have an ichthyologist on their staff who may teach systematics and distribution of fishes, but other fisheries courses are not always taught in the largest oceanographic institutions. From the viewpoint of a school of oceanography, the solution to most fisheries problems invariably involves a large scale, multivesseled, physical and chemical assault on a large part of the world ocean, because that is how the problem is conceived—by definition, of course.

California State Biologists' Struggle for Fishery Control

A belief prevalent early this century was that the oceans were inexhaustible and that man could not affect the species in the sea. These concepts were expounded by McIntosh, who was impressed by the "... extraordinary powers of reproduction of animals and plants in the sea ... and boldly asserted the inability of man to affect the species in the sea."[6] This general belief still exists (with some changes) at the present time. Others, however, felt that human activities could have a profound effect on living marine resources.[6]

Concerned with the protection of California's living marine resources, California state biologists consistently expressed concern about the rapidly growing exploitation of the sardine fishery. For example, as early as 1920, one such biologist, O. E. Sette, wrote about the sardine in Monterey Bay:

> The possibility of depletion cannot be much longer ignored. ... we have definite clues to the answers ... and it but remains ... to ... substantiate facts which we have concerning the age, rate of growth, migration and spawning. ... It now remains for continuance of this study to solve all the problems concerned, and insure the perpetuity of our great resource, through the adoption of intelligent conservational measures.[7]

The difficulties and frustrations encountered by the California Fish and Game Commissioners and their staff in attempting to gain control over the burgeoning sardine fishery are well documented in the publications and Biennial Reports of the California Divison of Fish and Game (later called the California Department of Fish and Game). This early history of the sardine industry (its growth, economics, and legal regulation) has been summarized by Schaefer et al.[8]

After the states of Oregon and Washington approved the use of sardines for reduction to fish meal in the 1930s, there were essentially no restrictions on the quantity of landings or the use made of them in the Pacific Northwest. Inasmuch as the California Legislature never delegated full authority for regulating the sardine fishery to the Fish and Game Commission, the Commission was forced to attempt to control the fishery through the exercise of the only authority the Legislature had delegated to it, control over the reduction fishery. Schaefer et al.[8] and

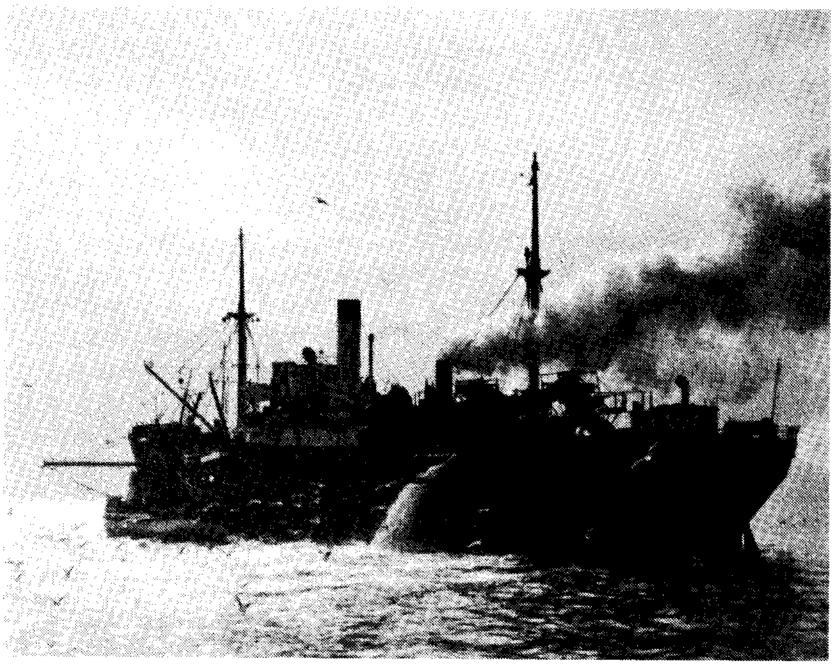

Figure 1 *Lake Miraflores,* the first reduction ship to operate outside the jurisdiction of the State of California, unloading sardines from a purse seiner in the early 1930s.

Ahlstrom and Radovich[9] have summarized the conflicts between canning and reduction interests and the desires of the Commission's biologists to protect the resource from overfishing and depletion.

During the 1930s, straight reductionists* bypassed State control over the reduction fishery by operating reduction ships outside the territorial sea limits, beyond the jurisdiction of the State of California.[9] (See Figures 1 and 2.) To stop the floating reduction plants, an initiative amendment to the California State Constitution was passed in November 1938 that prohibited any fishing vessel from operating in State waters if it delivered fish taken in the Pacific Ocean to points outside the State without authorization from the Commission. The enactment of this law, combined with lower fish oil prices and increased operating costs, ended reduction ship operations after 1938.[8]

As early as 1931, N. B. Scofield, the Chief of the Bureau of Commercial Fisheries of the California Division of Fish and Game, observed that

> the catch has not increased in proportion to the fishing effort expended, and there is every indication that the waters adjacent to the fishing ports have reached their limit of production and are already entering the first stages of depletion. The increase in the amount of sardines caught is the result of fishing farther from port with larger boats and improved fishing gear. . . .
>
> The Fish and Game Commission has consistently endeavored, through legislation and through cooperation with the canners, to restrict the amount of sardines which canners are permitted to use in their reduction plants with the belief that the canning of sardines is the highest use to which they can be put and that the excessive use of these fish in reduction plants would, in time, result in depletion of the source of supply. The majority of the canners, on the other hand, have sought to get quick returns from

---

*Straight reductionists were those who reduced all fish received from the fishermen, while canners reduced only a part of the catch consisting mainly of heads and offal.

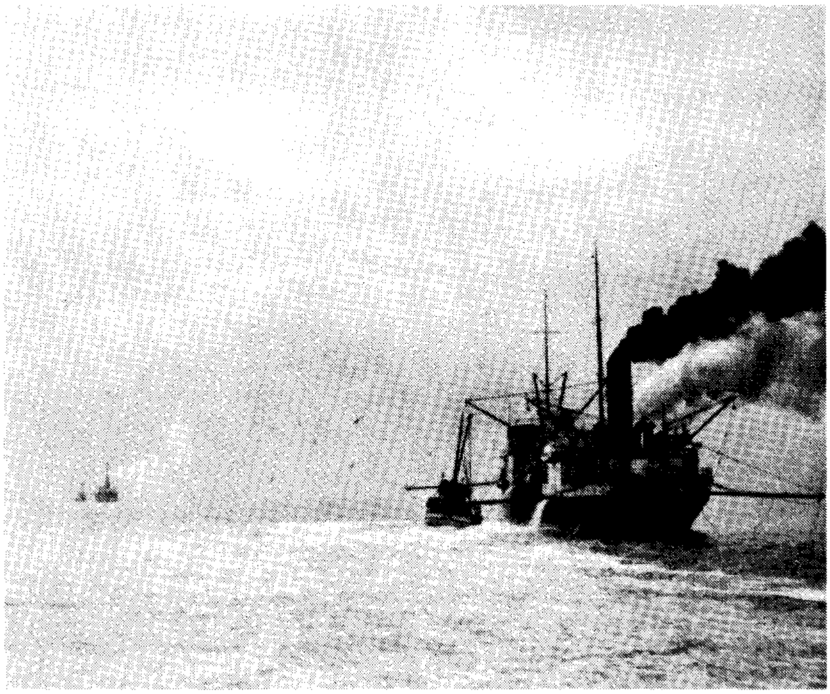

Figure 2 The reduction vessel, *Polarine,* unloading a purse seiner, with two other reduction ships anchored in the distance.

> sardine reduction and have made themselves believe there was no danger of depletion.[10]

In 1931, the State Division of Fish and Game advocated a seasonal limit of 200,000 tons on the amount of sardines that could be landed safely with little effect on the standing stock.[11] In 1934, N. B. Scofield[12] reiterated his view that the catch should be limited to 200,000 tons, indicating that this recommendation had been made 5 years earlier.

In 1938, W. L. Scofield[4] warned that overfishing was causing a collapse in the supply of sardines. He indicated that if the catch were cut to less than the amount replaced annually, the stock could rebuild back to its former productive level. He suggested 250,000 tons as the ideal level of catch. The 250,000 ton limit was also recommended by F. N. Clark,[13,14] who suggested that the limit might be raised somewhat during limited periods of exceptional spawning survival.

Prior to the 1938 initiative amendment to the State Constitution, which happened to coincide with the discontinuance of the reduction ships, an attempt had been made in 1936 to pass federal legislation either making it unlawful to take sardines for reduction on the high seas, or making such operations subject to the laws of the adjacent state. While this legislation was not passed, the attempt to pass it gave impetus to pressures for the establishment of a federal research laboratory on the Pacific Coast. W. L. Scofield[15] wrote:

> The [reduction] ship operators, foreseeing future legislation, resorted to a plan (used before and since) by which anti-reduction legislation could be postponed by asking for a special study of the abundance of sardines and thus disregard the work of the St. F. Lab. [State Fisheries Laboratory] or at least throw doubt upon its findings. The ship operators (mid-1930s) quietly promoted the plan of urging the legislatures of the 3 coastal states

> to ask Congress to have the U.S. Bureau [of Fisheries] make a study of sardine abundance. Wash. and Oregon complied but Calif. legislature refused to ask for Fed. [Federal] help. The U.S. Bur. was anxious to get a foothold in Calif. and sent out O. E. Sette (May 1937). This [was] a shrewd choice because Sette [was] a diplomat and personal friend of Calif. Lab. staff [actually he was a former state fisheries research biologist]. We told Sette he was not wanted in Calif. and asked him to go up to Wash. or Oregon who had asked for help.* Sette answered that he must work in Calif. because most of the sardines were here (not the real reason) and he pointed out that we could not afford to refuse our cooperation in a U.S. Bur. study of sardines. This was true and we had to grin and bear it. Sette started his sardine studies with a staff, housed at Stanford University. By 1938 a plan of cooperative sardine study for each agency was agreed upon.

From this beginning, the two agencies, one state and one federal, expended their efforts in different directions. On the one hand, the State's research biologists, with the responsibility for determining if and when "overfishing" was likely to occur and for making recommendations for appropriate management measures to prevent such overfishing, devoted their energies along those lines, even though their agency had not been delegated the authority to manage fully the commercial fishery. On the other hand, the Federal biologists, with no management responsibilities in (or obligations to) California, maintained a good rapport with the fishing industry, in that they were dedicated to assist the development and maintenance of a viable U.S. fishing industry, and looked for causes, other than fishing pressures, to explain the declines in the sardine fishery. This resulted in numerous debates at meetings and in conflicting scientific viewpoints in technical journals. The debates and conflicts were often based on the same data.

Despite warnings by State biologists that collapse of the sardine fishery was imminent, a large crop of young fish were produced in five successive years, 1936 to 1940 (Clark and Marr[16]). This gave rise to considerable speculation about the effect of environmental conditions on changes in the sardine population and to support for arguments by the fishing industry that nature, not the industry, caused much of the observed sardine population changes. The industry strongly supported the Federal biologists in their search for reasons, other than man, to explain the fluctuations in the sardine population.

The Marine Research Committee

After the large year-classes produced from 1936 through 1940 passed through the fishery, the sardine fishery collapsed to a low point in 1947 (Table 1). The fishing industry, concerned that legislation might be enacted to give the Commission control over the fishery, again resorted to the delaying tactic of advocating or sponsoring more research. In 1947, a meeting was held among representatives of the sardine fishing industry, United States Fish and Wildlife (later renamed U.S. Bureau of Fisheries), Scripps Institution of Oceanography, California Academy of Sciences, and California Division of Fish and Game. This group formu-

---

*W. L. Scofield related this incident to me, personally, as follows: "When Sette visited us after first contacting the major local fishing industry leaders, he asked how he could be of help to us. N. B. Scofield told him he could help us best by packing his bags and going back to Washington, D.C." O. E. Sette later personally confirmed this initial dialogue between the representatives of the two agencies.

lated a plan for a Marine Research Committee which would disburse funds collected from a tax on fish landings and would coordinate and sponsor research "to seek out the underlying principles that govern the Pacific sardine's behavior, availability, and total abundance."[17]

The Marine Research Committee was created by an act of the California Legislature in 1947, and was composed of nine members appointed by the Governor. Five members were specified to be selected from persons actively engaged in the canning or reduction industry, one member was the Chairman of the California Fish and Game Commission, one, the Executive Officer of the Division of Fish and Game, an additional member was taken from the Division of Fish and Game, and the ninth member was undesignated; the Director of the California Academy of Sciences was appointed to the undesignated position.

The work was to be carried out largely by Scripps Institution of Oceanography, U.S. Fish and Wildlife Service, California Division of Fish and Game, and the California Academy of Sciences, under the guidance of a technical committee representing the four agencies. Now there were two agencies: the Scripps Institution of Oceanography along with the Federal group, looking for reasons, other than fishing, to explain the sardine's decline; and State biologists also working, with mixed emotions, on a large-scale program. All of the above were somewhat under the auspices of a committee whose vote was controlled by the majority of five members from the sardine fishing industry.

The composition of the Marine Research Committee was changed in 1955 to consist of at least one member representing organized labor, at least one member representing organized sportsmen, two public members, and the same majority of five from the fishing industry.

The difference in perspectives of the biologists of the two fisheries agencies peaked in a joint paper by F. N. Clark (California Department of Fish and Game) and J. C. Marr (U.S. Fish and Wildlife Service)[16] in which the two authors drew different conclusions that were specifically identified from the same data. Also, the authors were careful to point out that the order of authorship was arranged alphabetically.

MORE RECENT RESEARCH EFFORTS

California Cooperative Oceanic Fisheries Investigations (CalCOFI)

Coordination of the efforts of the three principal agencies improved when the California Cooperative Oceanic Fisheries Investigations (CalCOFI) Committee was established in December 1957, with the working head of the unit in each of the three major agencies, Scripps Institution of Oceanography, the U.S. Bureau of Fisheries, and the California Department of Fish and Game, engaged in cooperative work. A fourth member, without voting power, was hired by the Marine Research Committee, and acted as Chairman.

Effects of Temperature on Population Size, Distribution, and Fishing Success

In 1957 dramatic changes in fish distribution revealed the close relationship of fish movements, fishing success, and local abundance of many marine species to seemingly subtle changes in average ocean temperatures.[18] Following these events and the World Sardine Conference that was convened in 1959 in Rome, in which the effects of fishing on the Pacific sardine were debated at length,[19] a change in attitudes of the two government agencies took place. California scientists became more aware of the effects of the environment, and Federal researchers began to appreciate that human activities could in fact adversely affect a pelagic marine resource.

At the 1959 Sardine Conference, Marr pointed out that a relationship existed between the average temperature from April of a given year to March of the following year and the sardine year-class size (Figure 3).[20] He also suggested that the northern anchovy, *Engraulis mordax* Girard, may prefer lower temperature optima than sardines. Radovich showed that up to the collapse of the fishery in the Pacific Northwest, ocean temperature correlated with an index of latitudinal distribution of young sardines (Figure 4) and that year-classes of more northerly originating sardines tended to contribute more heavily to the fishery (Figure 5).[21] Inasmuch as year-class sizes were estimated from the catch, it was not clear, then, to what extent Marr's correlation with temperature was due to year-class size or to effect of temperature on the latitudinal distribution of the origin of the year-class and the effect of its early latitudinal distribution on its subsequent vulnerability to fishing.

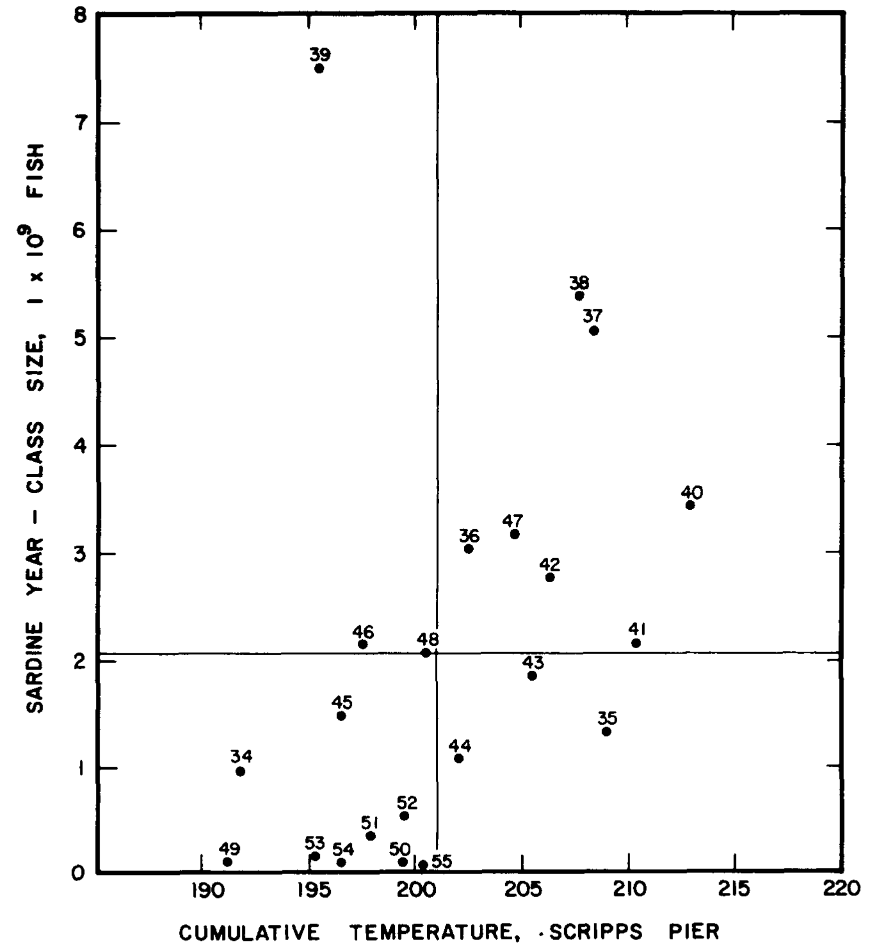

Figure 3 Relationship between year-class size and the sums of monthly mean sea temperature (April through March) at Scripps Pier. After Marr.[20]

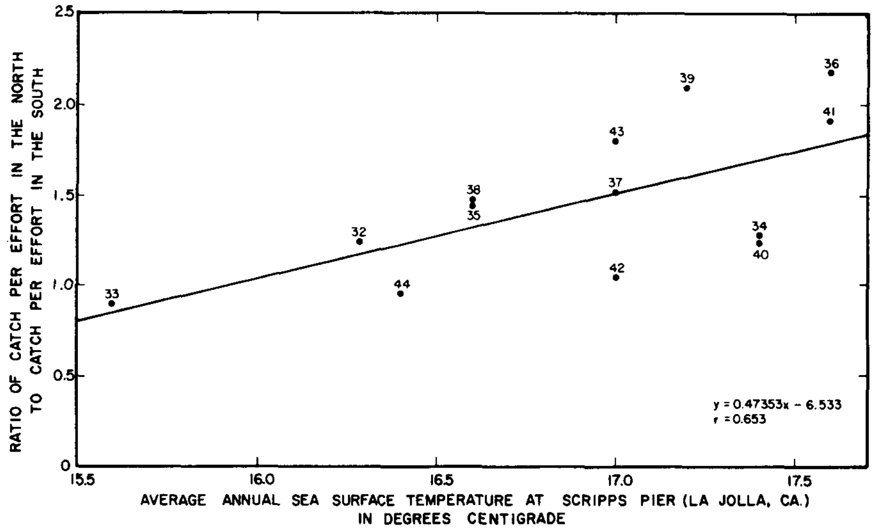

Figure 4 The relationship of sea surface temperatures at Scripps Pier to the index of north-south distribution of the Pacific sardine from the 1932–1933 to the 1944–1945 season. After Radovich.[21]

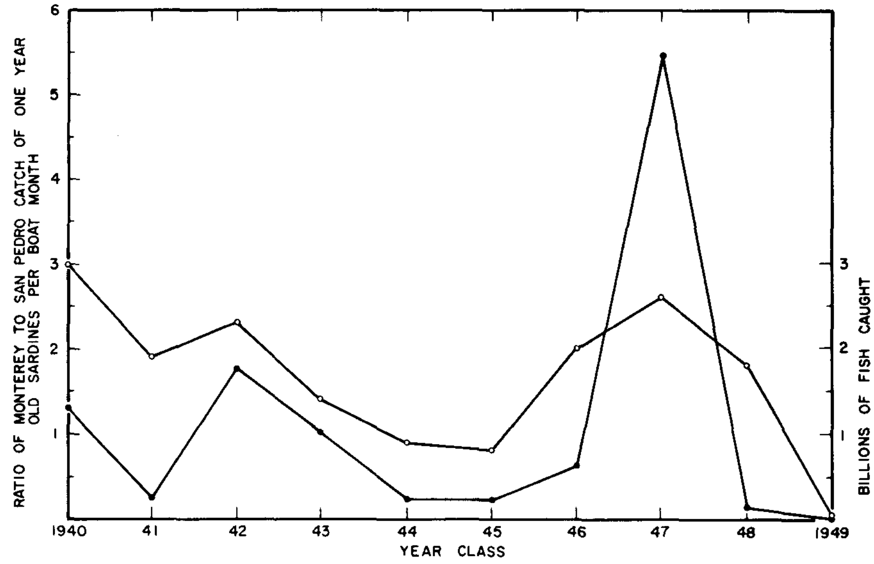

Figure 5 The ratio of the average lunar month catch at Monterey to the average lunar month catch at San Pedro of 1-year-old sardines (filled circles), and the cumulative total of each year-class of sardines taken in the fishery (open circles). After Radovich.[21]

Genetic Subpopulations

Another significant study resulted in delineating genetic strains of sardines by using erythrocyte antigens.[22,23] The studies agreed with Clark's conclusion that the sardine population from the Gulf of California and from the southern portion of Baja California were racially distinct from a single population to the north.[24] Vrooman[23] concluded that sardines from the Gulf of California, southern Baja California, and the northern California populations represented three distinct races, with a poorly defined (and somewhat variable) boundary separating the last two. Unfortunately, by the time that serological techniques had been

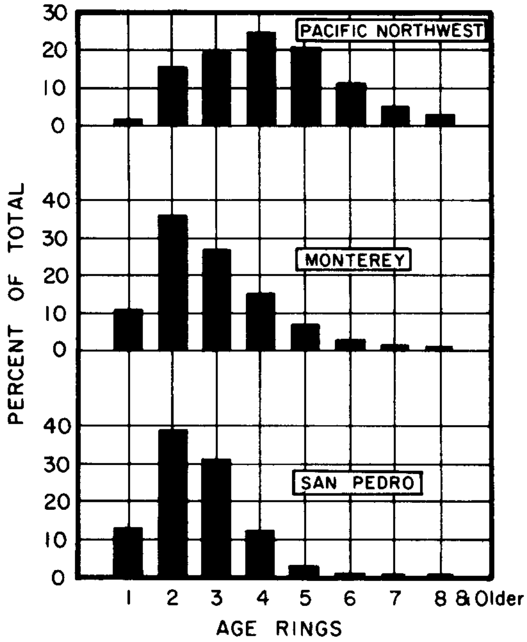

Figure 6 Average age composition of the Pacific sardine in different fishing areas during the 5-year period 1941–1942 through 1945–1946. After Clark and Marr.[16]

developed for separating genetic stocks, sardines had disappeared from the Pacific Northwest.

There were, however, two good lines of evidence to indicate that sardines from the Pacific Northwest and those from southern California did not mix randomly: (1) sardines in the Pacific Northwest were much larger and older than those in California (Figure 6); (2) there was a significant difference in scale types of fish from the two areas.[25] Whereas the northern type had relatively small growth during its first year, but grew more rapidly afterward, the California type scales represented a more rapid growth during the first year and a slower growth thereafter (Figure 7). Also, the northern type scales had well defined annuli (yearly rings) while the southern types had much fainter yearly rings.

Radovich, noting that the sardine temporarily restabilized at a much lower population regime following the decline in the Pacific Northwest (Figure 8), postulated that the stocks off the Pacific Northwest and off southern California were somewhat distinct, either genetically, or due to a strong tendency for fish to favor areas in which they were born (Figure 9).[26] He suggested that the fishery off the Northwest caught fish from the far northern stock during the summer, and that by winter much of this stock had moved off central California, where it was caught by California fishermen. The sizes and scale types of fish caught at these areas and seasons certainly suggested such a migration.[25] Scale types and sizes of fish also suggested that sardines caught in the fall off central California showed up off southern California in the winter the following year. J. L. McHugh (personal communication), in examining sardine samples from the Pacific Northwest and from California concluded, on the basis of meristic and morphometric variations, that fish from the two areas remained somewhat distinct from each other and did not mix to any great degree. The results of this study were never published.

Murphy rejected the existence of a far northern sardine stock by saying " . . . it is not necessary to invoke a third race to explain the

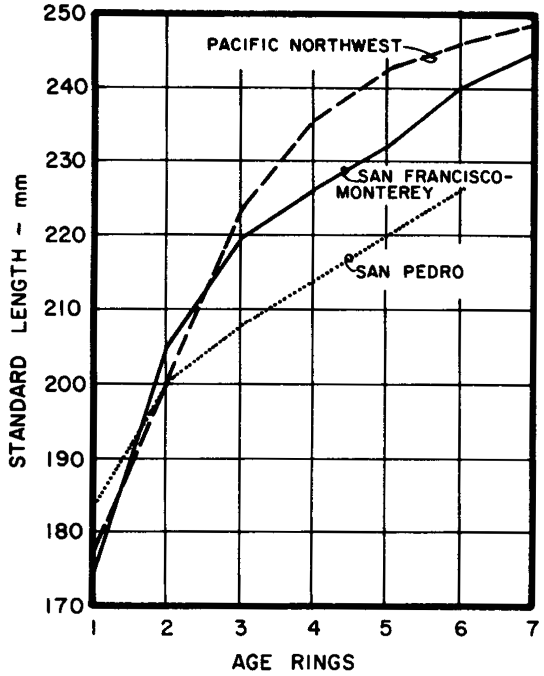

Figure 7 Observed growth curves (size on age) of sardines in several areas. After Clark and Marr.[16]

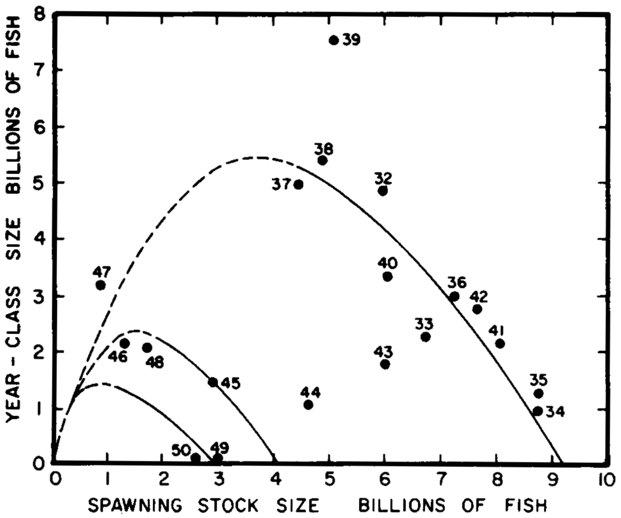

Figure 8 Hypothetical curves representing three probable regimes relating Pacific sardine year-class production to spawning stock size. After Radovich.[26]

collapse of the fishery."[27] He concluded that " . . . the observed quantitative changes in the population offer a sufficient explanation of events without introducing the undocumented qualitative change in the population." In doing so, he ignored the considerable body of evidence that demonstrated the stocks were not uniform or randomly distributed.

Sardine-Anchovy Interspecific Competition

During the period of the CalCOFI expanded program, it had become apparent that the anchovy population was increasing in size,[20] giving cause to speculation that the sardine and the anchovy populations may

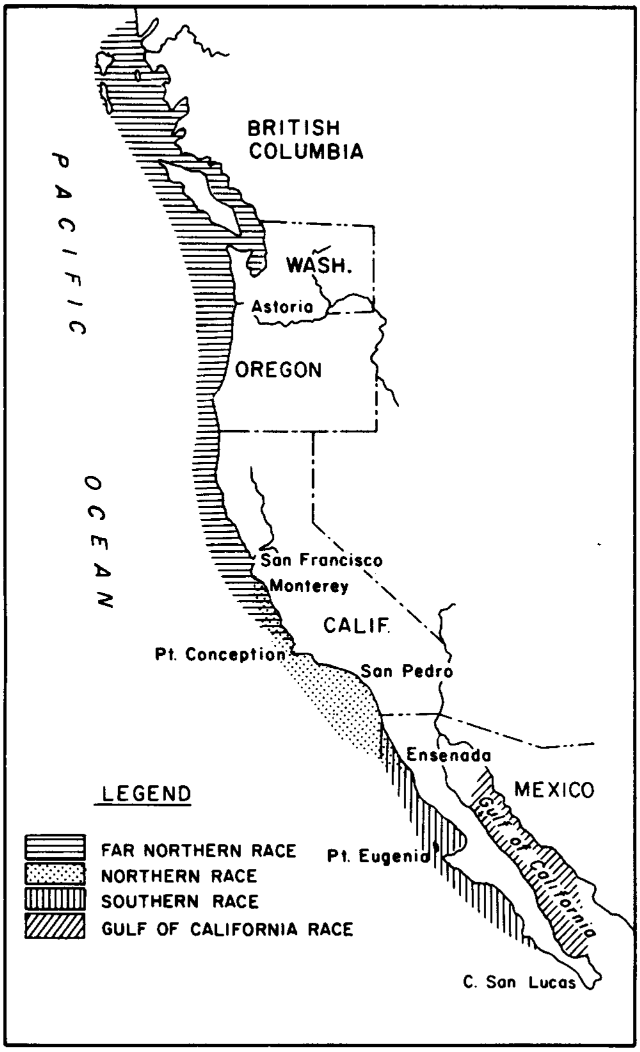

Figure 9 Diagramatic representation of four nonintermingling or partially intermingling stocks of Pacific sardines. The three stocks from the lower latitudes were delineated using arithrocyte antigens (Sprague and Vrooman,[22] Vrooman[23]); the far northern stock is suggested from studies of age and growth (Felin[25]) and population dynamics (Radovich[26]). Although the ranges are shown as overlapping, evidence suggests that the adjacent stocks did not generally occupy the same area at the same time. All stocks tended to range farther south during winters of cold years and farther north during summers of warm years.

be acting complementary to each other.[28] This speculation was based mainly on the increase in anchovy population in the 1950s, the co-occurrences and interrelationships of sardine and anchovy larvae in the California Current Region,[29,30] and the distribution of sardine and anchovy scales in the anaerobic sediments of the Santa Barbara Basin (off Santa Barbara, California).[31]

Murphy and Isaacs in a 1964 report to the Marine Research Committee,[32] estimated the anchovy abundance in southern California at that time at about one-half that of sardines in 1940 and 1941, and 6 times the abundance of sardines in the 1950–1957 period. They suggested that the decrease in sardines between the two periods had been balanced by increases in anchovies. Murphy presented an additional report at that meeting,[33] which also contained a table presenting anchovy and sardine larval catches from 1951 through 1959.

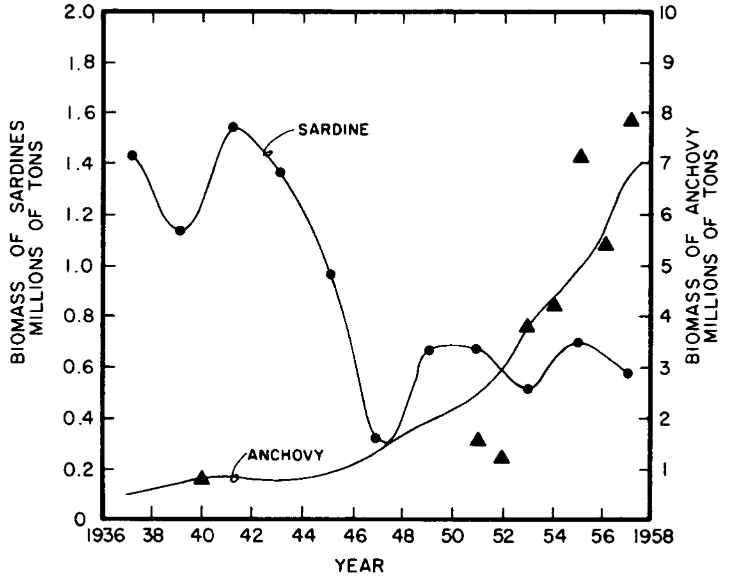

Figure 10 Annual biomass from 1936 to 1958 of the Pacific sardine and northern anchovy. The anchovy curve was generated by analog computer from Volterra competition equations and the sardine biomass was simulated using an analog computer method. After Silliman;[34] data from Murphy[33] and Murphy and Isaacs.[32]

Silliman[34] used data presented at the 1964 Marine Research Committee meeting and an analog computer to generate population curves of sardines and anchovies from Volterra competition equations (Figure 10).* He assumed competition for food to be the limiting factor for the combined biomasses of the two species. Only one point for the anchovy biomass prior to 1951 was used in this simulation, principally because the ichthyoplankton surveys of the CalCOFI program had not been fully implemented until 1951. The earlier point was in 1940 and resulted from the numbers of anchovy larvae taken in surveys made by Department of Fish and Game personnel then. Silliman's simulated curves have been cited in the literature as examples of competition and as substantiation of the Volterra competition equations.[35]

Smith indicated that the early cruises in 1940 and 1941 were conducted during the sardine spawning season and excluded an important portion of the anchovy spawning season.[36] In addition, the cruises only sampled 20% of the area that was later surveyed routinely. He derived total larva estimates for 1940 and 1941 for sardines and anchovies by comparing the 1940 and 1941 values with data obtained from analogous cruises in 1951 to 1960, conducted in the same season and covering the same area. His results (Table 2 and Figure 11) show his anchovy biomass values for 1940 and 1941 to be an order of magnitude higher than the value Silliman used. Smith concluded that both the anchovy and sardine populations declined between 1941 and 1951 and subsequently the anchovy population increased to over 5 million tons between 1962 and 1966. Smith's interpretation is the one commonly held at the present time by scientists working in the CalCOFI program, and is in direct contrast to the interpretation advanced by Silliman.

Murphy attributed the increase in the anchovy population to its use of the void left by the disappearance of the sardine.[27] He hypothesizes that

---

*The Volterra competition equations are based on the logistic curve and mathematically describe competition between organisms for food or space.

TABLE 2. Sardine and Anchovy Spawner Biomass Estimates by Ratio and Regression Methods

Year	Murphy Sardine Spawner Biomass (×10^3T)	Regression Sardine Spawner Biomass (×10^3T)	Sardine Larval Estimate (×10^{12})	Anchovy Larval Estimate (×10^{12})	Anchovy Sardine Ratio	Ratio Anchovy Spawner Biomass (×10^3T)	Regression Anchovy Spawner Biomass (×10^3T)
1940	1,296		1,634[a]	5,943[a]	3.64	2,359	
1941	2,001		2,476[a]	7,104[a]	2.87	2,871	
—							
1950	716		3,343	2,602	0.78	279	
1951	570	553	2,685	6,504	2.42	690	637
1952	554	542	2,633	8,132	3.09	856	797
1953	709	450	2,189 (3,442)[b]	13,632	6.23 (3.96)	2,209 (1,404)	1,335
1954	668	658	3,193	18,533	5.80	1,937	1,816
1955	425	404	1,959	17,100	8.73	1,855	1,676
1956	293	351	1,706	15,215	8.92	1,307	1,491
1957	212	234	1,137	20,040	17.63	1,869	1,964
1958	281	299	1,453	28,272	19.46	2,875	2,771
1959	190	117	570 (922)	23,463	41.16 (25.45)	3,910 (2,418)	2,299
1960		201	975	31,414	32.22		3,079
1961		132	642	32,538	50.68		3,189
1962		151	731	63,758	87.22		6,248
1963		78	379	61,533	162.36		6,030
1964		104	505	52,253	103.47		5,121
1965		226	1,098	79,292	72.21		7,771
1966		151	735				
—				52,200	71.02		5,116
1969		27[c]	132[c]	33,623[c]	254.72[c]		3,293[c]

[a] 1940, 1941—larval estimates seasonally adjusted.

[b] Parenthetic numbers for 1953 and 1959 assume larval numbers biased.

[c] 1969—larval counts 75% complete; adjusted for extra retention of small larvae.

After Smith.[36]

food was the major resource for which the two species were competing and, in fact, this assumption was the basis for Silliman's simulation.

It was demonstrated by Soutar and Isaacs that the occurrence of sardine and anchovy scales are aggregated throughout the 1,850 year record in core samples of sediments from the anaerobic Santa Barbara Basin, and that sardine scales have appeared a number of times with a duration of between 20 and 150 years and with periods of absence between occurrences on an average of 80 years.[37] Northern anchovy scales were found to be more abundant throughout the time series. The hypothesis that the Pacific sardine and the northern anchovy are direct competitors is not supported by the less than significant positive correlation between the scale deposition of the two species in the Santa Barbara sediment.[38]

Iles concluded that, because the growth rates of the smaller year-classes were higher, the decline in the sardine population was not due to a reduction in its food supply resulting from environmental changes.[39] He reasoned that the increase in the length of sardines suggests the environment was not saturated with sardines, and hence food was not a limiting factor. He concurred with Murphy,[27] that fishing rates for the sardine population lowered reproduction to an extent that a decline was inevitable and that it was improbable that the population would have declined in the absence of fishing pressures. Iles disagrees with Murphy's contention that the 1949 year-class marked the most significant change in population status. He concurred with Marr[20] that recruitment failure set in during the mid-1940s. Iles also contends that the rise of the anchovy population off California was in response to the environmental

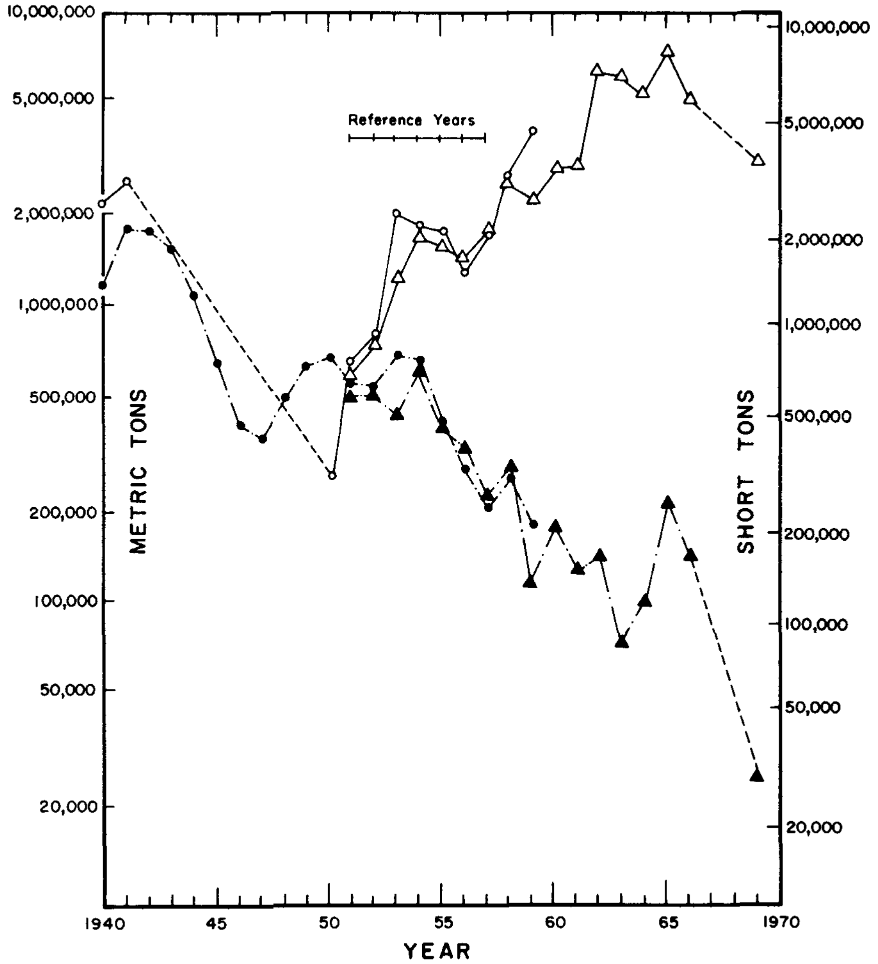

Figure 11 Sardine and anchovy biomass estimates from 1940 through 1969. The solid circle represents sardine biomass calculated from the fishery by Murphy.[27] The solid triangle represents sardine biomass derived from a regression estimate of the relationship between the Murphy biomass estimate and the annual total regional census estimate of sardine larvae during the reference years. The open circle represents the estimates of biomass derived from the ratio of anchovy larvae to sardine larvae and the Murphy sardine biomass estimate from 1940 to 1959. The open triangle represents anchovy biomass derived from a regression estimate of the relationship between the anchovy tonnage calculated from the anchovy to sardine larvae ratio and the annual total regional census estimate of anchovy larvae. Dashed lines represent interpolations between nonadjacent years. After Smith.[36] Compare with Figure 10.

void created by the decline of the sardine and not the cause of the decline.

Lasker has shown that, for the northern anchovy, food may be limiting at the critical time in the larval development when feeding first begins.[40] The presence of the proper food of the right size at the right density in the vicinity of the larva determines whether or not a larval anchovy survives past this critical stage. He has pointed out that extreme patchiness in the distribution of proper food exists in time and space. Upwelling may disperse the food concentrations so that, if it occurred at the critical time, a year-class failure would be a likely possibility. Inasmuch as sardine larvae and anchovy larvae feed on similar food, sardines may be affected similarly at the critical time of first feeding.

MacCall examined anchovy scales from sediments of anaerobic basins and found that the widths of scales during periods of high and low anchovy scale deposition did not differ significantly.[41] This suggested that intraspecific competition for food either did not affect growth rates or was masked by other factors. On the other hand, he found that anchovy scale widths from groups represented by periods of high sardine scale deposition rates were significantly smaller than those from groups based on periods of low sardine scale deposition rates. Anchovies seem to be smaller when sardines are abundant and larger when sardines are scarce. This may be due to interspecific competition for food, although other explanations are also possible. Increased selective predation on anchovies could result in a higher mortality and a smaller average length of the anchovy population. MacCall also pointed out that the record of the past century's abundance of sardine scales does not reveal a period of low abundance comparable to the present one and suggested that the present depletion was, therefore, not a natural one.[41]

Density-Controlling Mechanisms

If food does not appear to be the limiting factor related to poor sardine year-classes, except perhaps at the critical stage of first feeding after the yolk sac has been absorbed, then one should look for other density-controlling mechanisms for sardines and anchovies, such as predation and cannibalism. Hunter has found cannibalism of eggs by anchovies can account for about 50% of the total egg mortality.[42] The percentage would vary depending on the density of anchovies and of other food. Such a relationship would constitute a strong density-limiting force, and may well be the principal interaction between the two species. Sardines eat sardine eggs and larvae and anchovy eggs and larvae.[43]

Radovich suggested that, because man follows aggregations of schools and uses communication techniques to concentrate fishing effort on school groups, each nominal unit of fishing effort expended will take an increasingly larger portion of a declining pelagic fish population.[44–46] The catchability coefficient, then, is a variable function of the population.*

Radovich suggested that behavioral characteristics, such as schooling behavior, which have evolved through natural selection to decrease mortality from predation, may work toward the destruction of the prey

---

*MacCall used a power function to approximate the catchability coefficient[47]:

$$Q = \alpha N^{\beta}$$

where Q is analogous to the catchability coefficient, q, N is the mean population size, and α and β are constants.

$$C/f = QN$$

where C is the catch in number and f is the number of nominal effort units. If we assume the two previous equations, it follows that

$$C/f = \alpha N^{\beta+1}$$

At $\beta = 0$, the catchability coefficient is a constant and a linear relationship exists between catch-per-effort and population. At $\beta = -1.0$, C/f is a constant, and at all other values of β, C/f bears a curvilinear relationship to population size.

Fox calculated a β of -0.3 for the Pacific sardine fishery from 1932 to 1954.[48] MacCall estimated a β of -0.724 for the sardine.[47] With a β of these values, if effort is increased beyond a critical point, a population collapse is inevitable (Figure 12) instead of reaching some equilibrium as predicted by Schaefer's model.[49,50]

species when it is suddenly confronted by a fishery which evolves more rapidly than does the fishes' defense against it.[51]

THE END OF THE MARINE RESEARCH COMMITTEE

With the passage of the Fishery Conservation and Management Act of 1976, the United States established a conservation zone between 3 miles and 200 miles off the coast within which the United States has managment authority over fishery resources excepting tuna. The original utility to the fishing industry of the Marine Research Committee, that of forestalling managment of the resources, was somewhat removed.

Therefore, at the request of the California fishing industry, at the end of 1978, the Marine Research Committee was dissolved by an act of the California Legislature; however, by mutual agreement, the University of California, the National Marine Fisheries Service and the California Department of Fish and Game are continuing the California Cooperative Oceanic Fisheries Investigations as a viable cooperative research unit, beginning in 1979.

DISCUSSION

From the foregoing examination of only a small portion of the work which has been done on the Pacific sardine and the northern anchovy, it is apparent that most simplified generalizations are probably incorrect. Any model attempting to describe these populations must be consistent with the results of all the studies on these species. Following is a brief summary of the major points in this paper, all of which must be considered in any modeling attempt.

A model for sardines must account for a population heterogeneity of sardines that does not randomly mix throughout its geographic range. The evidence suggests the Pacific sardine consists of a clinal distribution of intraspecific populations in which there is limited intermingling and a series of variable overlapping coastal migrations of more than one stock.[25] Sardines in the Pacific Northwest were distributed farther north in the summer months when the fishery in that area operated.[52] During the winter months, many of these fish migrated south and were caught

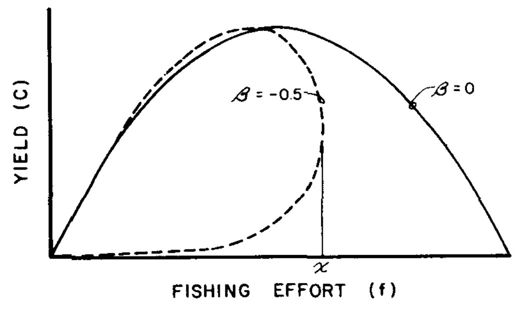

Figure 12 Effect of negative values of β on the equilibrium catch curve. At $\beta = 0$, the catchability coefficient becomes a constant and the usual parabolic relationship depicted by Schaefer[50] holds. If $\beta = -0.5$, as effort is increased above a critical point, x, the yield curve becomes unstable and the population collapses. Such an event appears to have happened with the Pacific sardine. After Fox.[48]

off San Francisco as winter fish.[14] Similarly, sardines located off Monterey in the fall supported the winter fishing off southern California. Following the collapse of the fishery off the Pacific Northwest, the winter fishery failed off central California. With the failure of the central California stocks, the southern California stock migrated into Mexican waters and became unavailable soon after the fall season began.[53]

The model should include the higher vulnerability of the northern stocks and the proper sequence of the stocks' decline, with the northern stocks declining first. Wisner was able to find only the southern (central Baja California) "racial" types in the southern California fishery by the period 1950–1959, as indicated by vertebral number.[54]

The model must be consistent with variable and somewhat independent spawning success for the different areas along the coast,[18,21,25] and with different vulnerability of the different stocks resulting from sardine movements from one fishing area to another during each fishing season.

The model must be able to handle major single-season population shifts such as occurred in 1954 and 1958.[21] It must be consistent with higher average spawning success and less variability in large populations, and with a more concentrated inshore distribution of spawn in lower populations.[21]

The model must consider the intraspecific density-dependent relationship that seems to have existed for the various sardine stocks.[26] It could speculate on the effect of sardine population size on anchovy growth rates, but there is no evidence of the effect of anchovy populations on sardine growth rates. It should include cannibalism, as a population limiting mechanism. It should relate ocean temperature to the distribution of spawn success, and should be able to explain the success of the far northern 1939 year-class and its exceptional contribution to the fishery.

The model must consider the effect of a variable catchability coefficient, which increases as the population declines,[47,48,51] or as a population becomes more available to the fishery.[21] It must also consider the effect on the population of any major change in the abundance of a strong predator.[51] It must consider the variability in the temporal and aerial distribution of proper feed in relation to larvae at the time of first feeding and, finally, it must be consistent with results of all the many studies that have been conducted to date. A detailed model should contain a number of generalizations, many of which complement each other, and some of which do not.

I have presented the beginning of a conceptual framework which, I believe, makes a strong case that the present scarcity of sardines throughout their range and their complete absence off the Northwest is not a natural condition but, instead, is an inescapable climax, given the characteristics and the magnitude of the fishery and the behavior and life history of the species.

REFERENCES

1 W. G. Clark, "The lessons of the Peruvian anchoveta fishery," California Cooperative Oceanic Fisheries Investigations Reports, No. 19, 57–63 (1977).

2 C. Smith, *San Diego Union,* January 1979, B-2 (Col. 1), B-5 (Col. 4).

3 W. A. Nierenberg, "Physics and oceanography," Richtmyer Memorial Lecture, New York, January 30, 1979.

4 W. L. Scofield, "Sardine oil and our troubled waters," *California Fish and Game,* **24**, 210–223 (1938).

5 A. D. MacCall, "Population estimates for the waning years of the Pacific sardine fishery," California Cooperative Oceanic Fisheries Investigations Reports, No. 20, 72–82 (1979).

6 W. F. Thompson, "The scientific investigation of marine fisheries, as related to the work of the Fish and Game Commission in southern California," *Fish Bulletin,* Calif. Div. Fish Game, No. 2, 1919.

7 O. E. Sette, "The sardine problem in the Monterey Bay district," *California Fish and Game,* **6**, 181, 182 (1920).

8 M. B. Schaefer, O. E. Sette, and J. C. Marr, "Growth of Pacific coast pilchard fishery to 1942," U.S. Fish and Wild. Serv., Research Report No. 29, 1951.

9 E. H. Ahlstrom and J. Radovich, "Management of the Pacific Sardine," in N. G. Benson, Ed., *A Century of Fisheries in North America,* Spec. Pub. No. 7, Amer. Fish. Soc., Washington, D.C., 1970, pp. 183–193.

10 N. B. Scofield, "Report of the Bureau of Commercial Fisheries," *Thirty-First Biennial Report for the Years 1928–1930,* Calif. Div. Fish Game, 1931.

11 N. B. Scofield, "Report of the Bureau of Commercial Fisheries," *Thirty-Second Biennial Report for the Years 1930–1932,* Calif. Div. Fish Game, 1932.

12 N. B. Scofield, "Report of the Bureau of Commercial Fisheries," *Thirty-Third Biennial Report for the Years 1932–1934,* Calif. Div. Fish Game, 1934.

13 F. N. Clark, "Can the supply of sardines be maintained in California waters?" *California Fish and Game,* **25**, 172–176 (1939).

14 F. N. Clark, "Measures of abundance of the sardine, *Sardinops caerulea,* in California waters," *Fish Bulletin,* Calif. Div. Fish Game, No. 53, 1939.

15 W. L. Scofield, "Marine fisheries dates," unpublished report, on file at California State Fisheries Lab., Long Beach, CA, 1957.

16 F. N. Clark and J. C. Marr, Population dynamics of the Pacific sardine, Progress Report, Calif. Coop. Ocean. Invest., 1 July 1953–30 March 1955.

17 California Cooperative Sardine Research Program, Introduction, Progress Report, 1950.

18 J. Radovich, "Relationship of some marine organisms of the Northeast Pacific to water temperatures particularly during 1957 through 1959," *Fish Bulletin,* Calif. Dept. Fish Game, No. 112, 1961.

19 H. C. Davis, "World sardine conference report No. 2—does fishing really affect abundance of sardines?" *Pacific Fisherman* (1959).

20 J. C. Marr, "The causes of major variations in the catch of the Pacific sardine, *Sardinops caerulea* (Girard)," World Scientific Meeting on the Biology of Sardines and Related Species, Proceedings, 3, 667–791, FAO, Rome, 1960.

21 J. Radovich, "Some causes of fluctuations in catches of the Pacific sardine (*Sardinops caerulea,* Girard)," World Scientific Meeting on the Biology of Sardines and Related Species, Proceedings, 3, 1081–1093, FAO, Rome, 1960.

22 L. M. Sprague and A. M. Vrooman, "A racial analysis of the Pacific sardine *(Sardinops caerulea)*, based on studies of erythrocyte antigens," *Annals of the New York Academy of Science,* **97**, 131–138 (1962).

23 A. M. Vrooman, "Serologically differentiated subpopulations of the Pacific sardine, *Sardinops caerulea,*" *Journal of Fisheries Research Board of Canada,* **21**, 691–701 (1964).

24 F. N. Clark, "Analysis of populations of the Pacific sardine on the basis of vertebral counts," *Fish Bulletin,* Calif. Div. Fish Game, No. 54, 1947.

25 F. E. Felin, "Population heterogeneity in the Pacific pilchard," *Fishery Bulletin, U.S. Fish and Wild. Serv.,* **54**, 201–225 (1954).

26 J. Radovich, "Effects of sardine spawning stock size and environment on year-class production," *California Fish and Game,* **48**, 123–140 (1962).

27 G. I. Murphy, "Population biology of the Pacific sardine *(Sardinops caerulea)*," *Proceedings of the California Academy of Sciences,* **34**, 1–84 (1966).

28 J. L. Baxter, J. D. Isaacs, A. R. Longhurst, and P. M. Roedel, "Partial review of and proposed program for research toward utilization of the California current fishery resources," California Cooperative Oceanic Fisheries Investigations Reports, No. 12, 5–9 (1968).

29 J. D. Isaacs, "Larval sardine and anchovy interrelationships," California Cooperative Oceanic Fisheries Investigations Reports, No. 10, 102–140 (1965).

30 E. H. Ahlstrom, "Co-occurrences of sardine and anchovy larvae in the California current region off California and Baja California," California Cooperative Oceanic Fisheries Investigations Reports, No. 11, 117–139 (1967).

31 A. Soutar, "The accumulation of fish debris in certain California coastal sediments," California Cooperative Oceanic Fisheries Investigations Reports, No. 11, 136–139 (1967).

32 G. I. Murphy and J. D. Isaacs, "Species replacement in marine ecosystems with reference to the California current," *Minutes of Meeting Marine Research Committee*, **7**, 1–8, March 6, 1964.

33 G. I. Murphy, "Notes on the harvest of anchovies," *Minutes of Meeting Marine Research Committee*, **11**, 1–6, March 6, 1964.

34 R. P. Silliman, "Population models and test populations as research tools," *BioScience*, **19**, 524–528 (1969).

35 E. P. Odum, *Fundamentals of Ecology*, 3rd ed., W. B. Saunders, Philadelphia, 1971, p. 226.

36 P. E. Smith, "The increase in spawning biomass of northern anchovy, *Engraulis mordax*," *Fishery Bulletin*, U.S. Nat. Mar. Fish. Serv., **70**, 849–874 (1972).

37 A. Soutar and J. D. Isaacs, "History of fish populations inferred from fish scales in anaerobic sediments off California," California Cooperative Oceanic Fisheries Investigations Reports, No. 13, 63–70 (1969).

38 A. Soutar and J. D. Isaacs, "Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias," *Fishery Bulletin*, U.S. Nat. Mar. Fish. Serv., **72**, 257–273 (1974).

39 T. D. Iles, "The Interaction of Environment and Parent Stock Size in Determining Recruitment in the Pacific Sardine, as Revealed by Analysis of Density-Dependent O-Group Growth," in B. B. Parrish, Ed., *Fish Stocks and Recruitment*, Rapports Et. Procès-Verbaux Des Rèunions, Cons. Inter. Explor. Mer, Vol. 164, 1973, pp. 228–240.

40 R. Lasker, "The relation between oceanographic conditions and larval anchovy food in the California current: Identification of factors contributing to recruitment failure, Rapports Et. Procès-Verbaux Des Rèunions, Cons. Inter. Explor. Mer, **173**, 212–230 (1978).

41 A. D. MacCall, "Recent anaerobic varved sediments of the Santa Barbara and Guaymas basins with special reference to occurrence of fish scales," Southwest Fisheries Center, U.S. Nat. Mar. Fish. Serv., La Jolla, CA, Admin. Report No. LJ-79-24 (1979).

42 J. R. Hunter, "Egg cannibalism in the northern anchovy," unpublished manuscript, Southwest Fisheries Center, U.S. Nat. Mar. Fish. Serv., La Jolla, CA.

43 C. H. Hand and L. D. Berner, "Food of the Pacific sardine *(Sardinops caerulea)*," *Fishery Bulletin*, U.S. Fish and Wild. Serv., **60**, 175–184 (1959).

44 J. Radovich, "A challenge of accepted concepts involving catch-per-unit-of-effort data," *Cal-Neva Wildlife Transactions*, 64–67, 1973.

45 J. Radovich, "An Application of Optimum Sustainable Yield Theory and Marine Fisheries," in P. M. Roedel, ed., *Optimum Sustainable Yield as a Concept in Fisheries Management*, Amer. Fish. Soc., Spec. Pub. No. 9, 1975, pp. 21–28.

46 J. Radovich, "Catch-per-unit-of-effort: Fact, fiction or dogma," California Cooperative Oceanic Fisheries Investigations Reports, No. 18, 31–33 (1976).

47 A. D. MacCall, "Density dependence of catchability coefficient in the California Pacific sardine, *Sardinops sagax caerulea*, purse-seine fishery," California Cooperative Oceanic Fisheries Investigations Reports, No. 18, 136–148 (1976).

48 W. W. Fox, Jr., "An overview of production modeling," Southwest Fisheries Center, U.S. Nat. Mar. Fish. Serv., La Jolla, CA, Admin. Report No. 10, 1–27 (1974).

49 M. B. Schaefer, "Some aspects of the dynamics of populations important to the management of the commercial marine fisheries," *Inter-American Tropical Tuna Commission Bulletin*, **1**, 26–56 (1954).

50 M. B. Schaefer, "A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean," *Inter-American Tropical Tuna Commission Bulletin*, **2**, 247–285 (1957).

51 J. Radovich, "Managing Pelagic Schooling Prey Species," in H. Clepper, Ed., *Predator-Prey Systems in Fisheries Management*, Sport. Fish. Inst., Washington, D.C., 1979, pp. 365–375.

52 F. E. Felin and J. B. Phillips, "Age and length composition of the sardine catch off the Pacific coast of the United States and Canada, 1941–42 through 1946–47," *Fish Bulletin,* Calif. Div. Fish Game, No. 69, 1948.

53 California Cooperative Oceanic Fisheries Investigations, *The Sardine Fishery in 1956–57,* Progress Report, 1958.

54 R. L. Wisner, "Evidence of a northward movement of stocks of the Pacific sardine based on the number of vertebrae," California Cooperative Oceanic Fisheries Investigations Reports, **8**, 75–82 (1961).